Modeling leaf phototropism in a cucumber canopy

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Introduction

In many species, it can be observed that plants actively adjust the exposition of their leaves into the direction of the incoming radiation, a phenomenon termed phototropism. This results in increased light utilization and higher plant productivity. Shade avoidance responses may be highly adaptive in a natural setting to help plants out-compete neighboring vegetation, but for many crop species a reallocation of resources can reduce crop yield. In maize, where in recent years yield gains have largely come through the breeding of varieties with reduced shading responses, at least some reactions to light gradients can be beneficial to crop performance (Maddonni et al. 2002). Cucumber hypocotyls respond to light signals with a high developmental plasticity (e.g., Shinkle et al. 2005) and wild-type cucumber plants preferentially project leaf area into light gaps and avoid poorly illuminated sites (Ballaré et al. 1995). Based on the data of an experiment conducted in spring 2006, we want to conceptualize and parameterize an extension of the cucumber L-system (Kahlen 2006) that takes into account the plant response to green shading.

Model

The presented model is an extension of the original L-system for cucumber (Kahlen 2006), designed to predict photomorphogenic responses of canopy elements induced by gradients in the local light environment. The model uses the absorbed photosynthetically active radiation (PAR) of the two leaf halves to detect a gradient in PAR between the sunlit parts on the left and right leaf half, LPAR and RPAR. This gradient acts as the driving force for the differential growth response of the corresponding petiole. The response to this gradient leads to tropic movement of the lamina.

For the simplicity of the model, incoming PAR is perpendicular to the ground with a constant intensity of 500 µmol m^{-2} s^{-1}. This corresponds to the mean PAR inside a greenhouse on a sunny summer's day in Germany. Each time step phyllochron is increased by 1. A leaf is visualized by a set of contiguous triangles with a predefined area distribution. It is assumed to reflect 6 % and transmit 7 % of the incident PAR. Each triangle perceives PAR via its corresponding communication module. On leaf level, PAR is assumed to be the mean triangle PAR weighted by the triangle areas. The leaf PAR per phyllochron is converted to the increase in leaf dry weight per phyllochron assuming a day length of 14 h, a phyllochron of 1.3 days, a light use efficiency of 3.4 g MJ^{-1} and an energy equivalent of $0.235 \cdot 10^6$ J per mol of photons. In addition, the model assumes a threshold temperature sum of 136 °Cd for leaf expansion. When reaching this value, a leaf stops expanding. In contrast to the model of Kahlen (2006), maximum leaf area is not an input variable anymore. Leaf area results from leaf dry weight calculated as the ratio of leaf dry weight over specific leaf area, SLA. SLA is assumed to be constant, e.g., 300 cm^2 g^{-1} in the case of two plants per m^2 in row distribution (Kahlen and Stützel 2007). An allometric relationship derived from Kahlen and Stützel (2007) is used to calculate petiole length from lamina dry weight. A linear relationship between leaf area and leaf length is used to calculate leaf length. All lengths used to construct the lamina triangulation are proportional to leaf length. The deviation angle from the initial azimuth orientation of a leaf due to leaf tropism is termed tropism angle. The tropism angle is calculated in relation to the LPAR:RPAR ratio and the petiole age. The maximum angle resulting from differential growth is assumed to be 30°

per phyllochron. If the thermal age of the petiole exceeds 153 °Cd, differential growth stops. The leaf moves to its left side, if the LPAR:RPAR ratio is greater than 1. Else, it moves to its right side. The zone of differential growth of a petiole is located in close vicinity to the intersection of petiole and stem. The bending of up to 90° occurs on a length of a few centimeters. In the model, the tropism angle results in a bending of the basal part of the petiole.

Simulation

The L-system production rules are interpreted by the program CPFG implemented in the software L-studio 4.0.54 (e.g., Měch 2004). The distribution of light in the canopy is simulated using the classical radiosity model integrated in the interface CARIBU 4.4. Only direct lighting on a finite view reduced by reflection and transmission is used. Four scenarios were considered: One and two plants per m^2 grown in rows with and without the option for leaf tropism. Each virtual canopy consisted of five plants in a row. Thus, two plants were border plants. The plant in the center of these small canopies is termed 'center plant'. Simulations were done for 15 phyllochrons.

Evaluation of the model

Simulated leaf tropism in the case of the dense canopy led to a realistic restructuring of the whole canopy (Fig 1). The leaves moved away from the poorly illuminated to the sunlit gaps in the canopy. This means, a leaf did not maintain its orientation when it was in line with the main row axis. Leaves growing perpendicularly to the main row axis did not move at all as were already in their 'optimum' light environment.
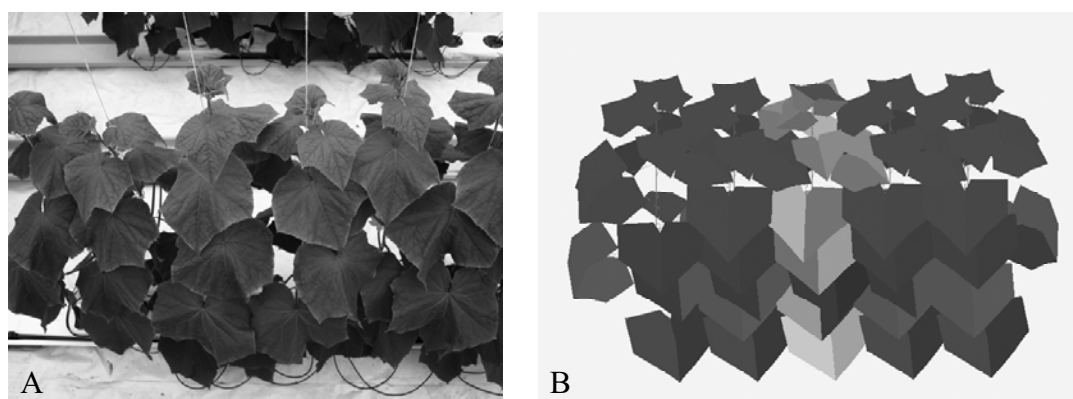

Fig. 1. A) Photograph of a cucumber canopy with two plants per m^2 in row distribution. Plants were vertically trained by clips which do not disturb the reallocation of the leaves. B) Simulation of a cucumber canopy in the same distribution at phyllochron 15. Left and right leaf halves are colored differently. The center plant is colored individually, because it represents a typical canopy plant.

In all simulations, the initial azimuth orientation of a leaf was not affected by the plant distribution. But, we observed in the simulation of the dense canopy both: two consecutive leaves may move either to opposite or to the same side of the row (Fig 1). In contrast, allowing leaf tropism in the wide canopy did not affect single leaf orientation (picture not shown). All effects were observed in the experiment, too. One consequence of the simulated leaf tropism in the dense canopy is that all leaves reaching an age of ca. eight days can increase (e.g., leaf 3 in Fig 2A) or maintain (e.g., leaf 6 in Fig 2A) the mean leaf PAR in comparison to the mean leaf PAR in the simulation without leaf tropism. This might be of particular importance for a plant, because a lamina of this age reaches its maximum net photosynthetic rate (Wiechers, pers. comm.). The simulation also shows that, leaf tropism is beneficial for PAR absorption on plant level, too. In comparison to the normalized PAR of the dense stand, mean PAR of the wide stand is higher (Fig. 2B).
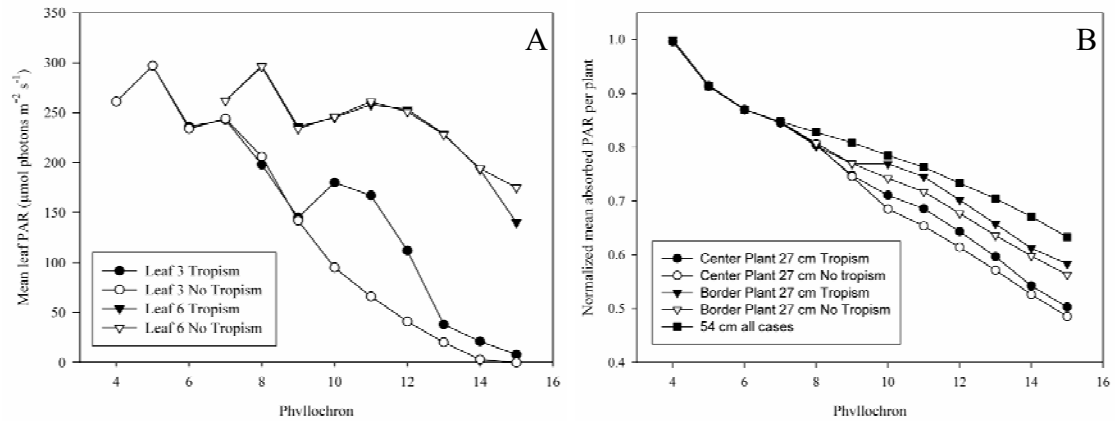
Fig. 2. A) Simulated mean absorbed direct PAR of leaf 3 and 6 in relation to phyllochrons. The leaves are parts of the center plant grown in a virtual canopy with 2 plants m^{-2} and row distribution with a distance between neighboring plants within the row of 27 cm. 'No tropism' means that plants were not allowed to reorient their leaves due to mutual shading. B) Simulated normalized mean absorbed direct PAR per plant in relation to phyllochrons.

Conclusions

The software L-studio and the interface CARIBU established the basis for the presented functional-structural model of cucumber. Even in its preliminary form, it can be used to simulate photomorphogenic canopy responses induced by gradients in the local light environment of the individual leaf. The model advances the state of the art in canopy modeling by considering leaf reorientation as triggered by a stimulus and the plant's response in terms of petiole bending. In future, some model features will have to be improved, e.g., the petiole bending by differential growth and the model time step to keep track of the sun position, because our eventual goal is to use a model to identify improved greenhouse cucumber production systems.

Acknowledgments

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